

The Philippines in Wallacea

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Abstract: The Philippine archipelago's position in Wallacea has been a matter of debate and is a biogeographic problem that has never been fully settled. In the current review this problem is examined in light of comparative phylogenetic biogeography, tectonic history and panbiogeography. The information about these supports Dickerson et al. (1928) assertions on the faunal transition character of Wallacea and how this defines the biotic regions of the Philippines within Wallacea and its links with Sulawesi. There is a need to go beyond the Pleistocene paradigm in Philippine biogeography if a fuller understanding of the scale and dimensions of biodiversity in the Philippines is to be achieved.

Key words: Philippines, Wallacea, comparative biogeography, panbiogeography, Sulawesi.

Introduction

The Philippines is an archipelago of approximately 7000 islands in the Western Pacific (Fig. 1). The position of the archipelago with respect to Wallacea (Dickerson et al. 1928) has been a subject for debate in biogeography. Wallacea is defined to be the region between Wallace's Line in the west and Weber's Line to the east (Fig. 2). The original Wallace's Line delineated the islands west of the line. Huxley's modification of the line included all the oceanic islands of the Philippines east of the line (Mayr 1976; Simpson 1977). Wallace (1880) considered the islands to be part of the Oriental region but was separated from the Asian mainland at a very early date (Simpson 1977). Dickerson et al. (1928) placed the Philippines as the northern apex of the Wallacean "triangle". While traditionally Wallace's Line delineated the Asian biotic region from the Australian and Weber's Line delineated the Australian from the Wallacean, Dickerson et al (1928) considered Wallacea as a faunal transition zone largely depauperate in Asian and Australian representatives (Wallace 1880; Mayr 1976) but characterized by a significant degree of novel and relict endemism.

In this paper the position of the Philippines with respect to Wallacea is examined under the present theories of phylogenetic biogeography and the tectonic setting and reconstruction of the archipelago. The significance of the Gondwanan affinities of Philippine taxa shared with Wallacea will be assessed using a panbiogeographic framework.

The physical geographic, tectonic and biogeographic setting of the Philippines

Physical geography

The Philippine archipelago can be divided into three groupings, Luzon, Visayas and Mindanao. Mindanao and Luzon are the two largest islands of Philippine archipelago. Luzon is the largest and most populous island of the Philippines with an area of 104688 km². It is orientated latitudinally from 18N to 12N and longitudinally from 119 to 123E. Mindanao is the second largest (97530 km²) and most easternmost island in the Philippines. The island is orientated more longitudinally (121E to 126E) unlike Luzon. Luzon has four major mountain systems, the Eastern Sierra Madre, Caraballo, Central Cordillera and Zambales ranges. Mindanao has the most complex physiography of the Philippine islands. There are 5 mountain range systems on the island mainly of volcanic origin and correspond to the crustal blocks identified. The highest Philippine mountain, Mount Apo is located along the eastern region of the island. Luzon is composed of 7 crustal blocks while Mindanao has 6 crustal blocks. Luzon and Mindanao are separated by the Visayas islands, the second major geographical groupings. The major islands are part of the Philippines "hotspot" of biodiversity (Heaney et al. 1998). Luzon and Mindanao formed their respective Greater islands during the Pleistocene. Greater Luzon included the islands of Polilio and Catanduanes while Greater Mindanao included the Visayan islands of Samar and Leyte as well as Dinagat and Basilan islands. The Sulu



archipelago while culturally linked with Mindanao was never physically connected to it.

The Visayas is composed of the major islands of Panay, Negros, Masbate, Cebu, Samar and Leyte. Panay, Negros, Masbate and Cebu formed the Pleistocene island of Negros-Panay. Islands that have never been connected to Luzon, Mindanao or to other Visayan islands include Mindoro, Palawan, Sibuyan, Romblon, Tablas, Camiguin, Batanes islands, and the Babuyan islands. With the exception of Mindoro and Palawan, these islands are oceanic islands. Palawan is a fragment of continental crust which was separated during the formation of the South China Sea basin. This island was connected to Borneo for a time.

Tectonic history (Fig. 3)

The tectonic histories of the Philippine islands have been described by Hall (1996; 1998), Yumul (2008), for the Visayas by Dimalanta et al. (2006), and Yumul (2000). The convergence of Eurasian

plate and the Philippine plate resulted in a complex suite of tectonic features which include trenches and subduction zones on the eastern and western boundaries of the archipelago. The archipelago's western edge is bounded by the Manila trench and Negros-Sulu and Cotabato trenches. The South China Sea, Sulu Sea and Celebes Sea basins are subducting in this region. In the eastern region, the Philippine trench marks the site where the Philippine plate is subducting. The resulting stresses caused the formation of the Philippine Mobile Belt which is defined by the 1200 km long Philippine Fault.

The evolution of the archipelago began in the Mesozoic when a fragment of the Asian continent was fractured as a result of the birth of the South China Sea. This block gave rise to Palawan. Continued seafloor spreading and formation of oceanic crust in the Oligocene to the Miocene gave rise to the South China Sea. The formation of ophiolitic and arc rocks continued throughout the Tertiary. Widespread evidence of volcanic activity in the Southern region of Luzon and Central Visayas indi-



Figure 1. The Philippine archipelago.

cate continued subduction (McDermott et al. 2005; Vogel et al. 2006) in the Miocene. Before the Pliocene, the Philippines are widely hypothesized as part of an arc system at the edge of the Philippine plate. Paleomagnetic data suggests that the clockwise rotation and northward movement of the Philippine Plate was crucial to the genesis of Luzon. Luzon was once situated at subequatorial latitude as evidenced by paleomagnetic data of Central Cordillera ophiolites (Queaño et al. 2009). Northwestward rotation started in the Cretaceous. The formation of the Visayan Islands occurred in the Miocene to Pliocene (Fig. 2). These islands are composed of a melange of ophiolitic rocks and thus have a heterogeneous character (Faustino et al. 2003). Panay has thick sedimentary basins composed of Oligocene to Recent sedimentary rocks and the Panay western cordillera is hypothesized as crustal boundary between the Palawan microcontinental and Panay oceanic crustal blocks (Zamoras et al. 2008). The Visayas is separated from Mindanao by a proto-trench in the Bohol Sea (Faustino et al. 2003). The Zamboanga Peninsula is a microcontinental block with a Miocene origin and may have been part of Palawan (Yumul et al. 2004) and areas east of this block is composed of younger ophiolitic deposits (Hall 1996; 1998). Southern and Central Mindanao is characterized by a complex post collisional tectonic setting. A major collisional event that is reflected in the region's geology is the Cota-

bato Fault. This structure separates southern, central and northern Mindanao and is a boundary of crustal accretion (Middleton et al. 2004). Thus the major Philippine islands show evidence of crustal accretion and collision (Yumul et al. 2000; 2008).

History of biogeographic theories on the Philippines and their relevance to Wallacea

The biogeography of the Philippines is central to understanding Wallacean biogeography. This has remained a problem since Alfred Russel Wallace (Wallace 1859; 1880) described the distribution of biota in Southeast Asia. The floristic and faunal affinities of the Philippines are largely oriental in character as Wallace recognized but the archipelago lacks many of the representative oriental species (except in Palawan) and contains a significant Australian floral component which is best represented in Mindanao, especially in its eastern region. The faunal component has a high proportion of endemics. With these characteristics, the Philippines forms part of Wallacea (Dickerson et al. 1928).

The modern theory to account for Philippine terrestrial biodiversity is premised on island accretion or integration (Fig. 4) (Hall 1998) as a major factor in the evolution of high biodiversity (Heaney 1986; 1998; 1999; 2000; 2004; Heaney et al. 1990; 1998). The theory on the dimensions and

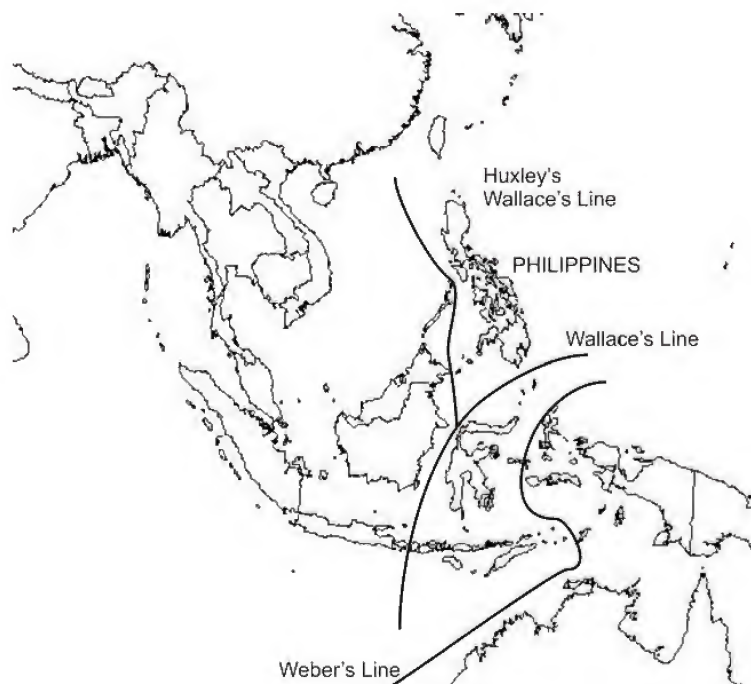


Figure 2. The Philippines with respect to zoogeographical boundaries in Southeast Asia.



origins of Philippine biodiversity is well developed (Heaney 1986; 1998; 1999; 2000; 2004; Heaney et al. 1990; 1998; 2005). The results of molecular biogeographic studies on mammals support the earlier predictions on colonization and *in situ* diversification (Steppan et al. 2003). In describing the biogeography of the region, terrestrial biogeographers have built upon the equilibrium theory of island biogeography (Macarthur et al. 1967).

Luzon's biogeography has been described by Merrill (1923) when he identified the following floral regions or subprovinces (Fig. 5). These are the 1) Eastern Luzon-Bicol peninsula region, 2) Luzon lowlands, 3) Central Cordillera, 4) Zambales mountains. Merrill describes Mindanao by delineating the island into its floral subprovinces which include 1) Eastern Mindanao, 2) Bukidnon-Kitanglad Highlands, 3) Zamboanga Peninsula and 4) Sulu Archipelago.

A biogeography of Mindanao is key to understanding the origins of the eastern Philippine biota and its phylogenetic affinity and connection with Sulawesi, the Maluku islands and New Guinea. This biotic region extends to eastern Luzon. Dickerson (1927) observed that the eastern region of the Philippines has a general climate characteristic and physiography. It is worth noting that the national icon of Philippine biodiversity, the Philippine Eagle

(*Pithecophaga jefferyi*) ranges from Mindanao to northeastern Luzon but is not recorded from Luzon's Bicol peninsula.

Dickerson et al. (1928) and Merrill (1923) delineates the eastern Philippines (including northeastern Luzon, Bicol, Samar, and Leyte) and Mindanao floristic region as "Philippine" for it has a high percentage of endemics. The other floristic regions are the Bornean and Formosan (Himalayan) based on its affinities to continental Asia. However, Mindanao can be further classified into subregions due the presence numerous pockets of endemism in the central plateau and the Bukidnon highlands. This highland region contains some herbaceous plants of northern affinity.

Merrill (1923) despite the lack of botanical records for the eastern Philippines recognizes this region as the distinct Eastern Philippine province. Among the hypotheses he proposed to account for this is the presence of a non distinct dry season and the mainly mountainous habitat of the eastern Philippine seaboard. The eastern side of Mindanao is also called as the "Eastern Mindanao Corridor". Aside from the eastern Philippine characteristic of Mindanao, the western section defined by the Zamboanga Peninsula has a striking botanical affinity to Borneo. This area roughly corresponds to the micro-continental fragment that accreted with the rest of

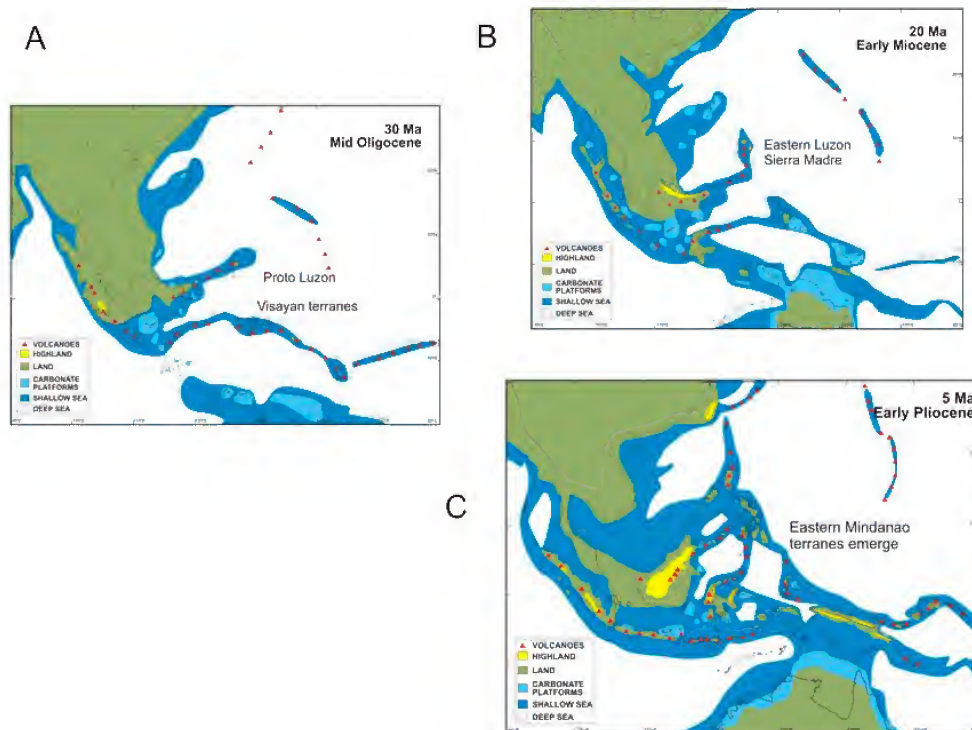


Figure 3. Tectonic evolution of the Philippines.

The oldest island is Luzon while the youngest terranes are found in Mindanao (adapted from Hall 1996).



Mindanao in its geological evolution.

The faunal regions, or provinces, of the Philippines have been described by Heaney and co-researchers as based on their 40 years of faunal surveys and studies (Heaney 1986; 1998; 1999; 2000; 2004; Heaney et al. 1990; 1998; 2005). The centres of endemism are coincident with the physiography of the greater islands of Luzon, Negros-Panay, Palawan, Mindoro and Mindanao during the Pliocene and Pleistocene sea level regressions. These greater islands were never connected to each other and served as centres for endemism.

Based on Heaney's research, Mindanao is considered as one faunal province with its formerly connected islands of Bohol, Samar, Leyte, Dinagat

and their associated small islands. However, Dickerson et al. (1928) recognized that Mindanao itself can be further subdivided into at least 4 faunal and floristic regions or subregions. First is the eastern region which includes the Agusan, Davao and Misamis political regions and the islands of Samar, Leyte and Dinagat. The second region is the south-eastern section of the island, consisting of the political subdivisions of Maguindanao, Cotabato, Sultan Kudarat. The third region consists of the Bukidnon highlands and the fourth, the Zamboanga Peninsula and Basilan. Sulu and Tawitawi are not considered part of Mindanao but as an independent faunal province.

In the other Philippine faunal and floral re-

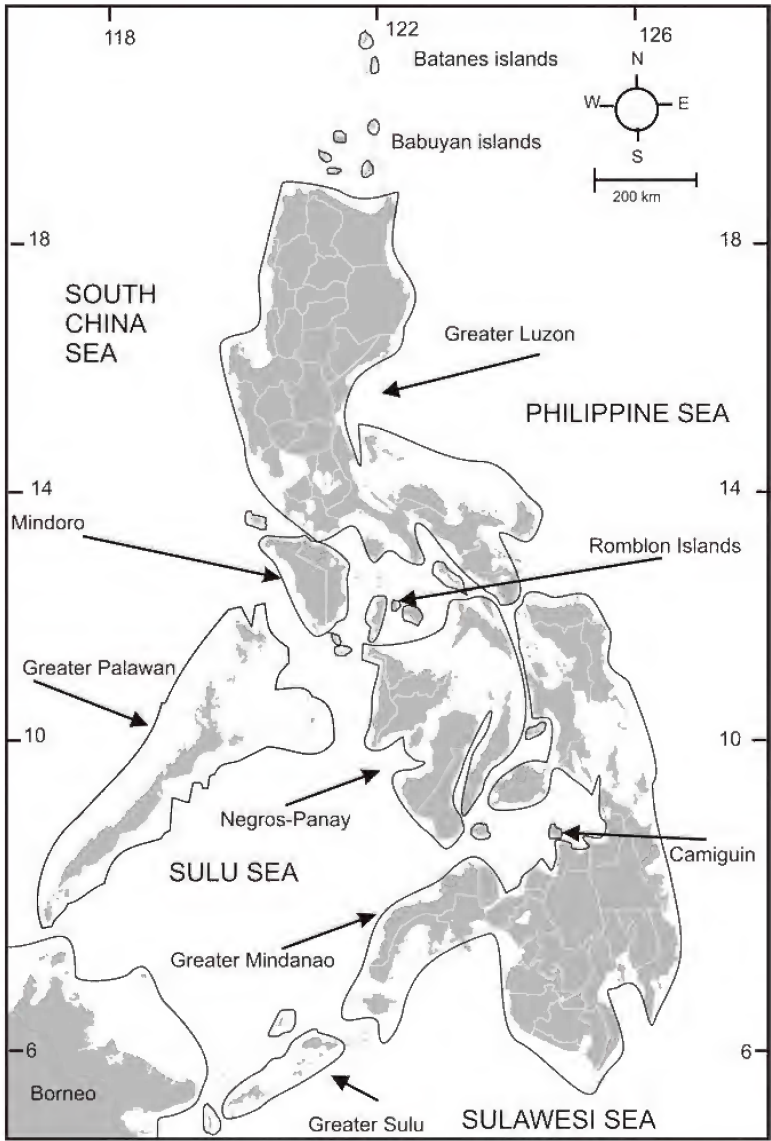


Figure 4. Pleistocene aggregated islands of the Philippines as based on the 150 m bathymetric line (adapted from Heaney 1986).



gions, Dickerson et al. (1928) initial classifications are generally concordant with Heaney's. However the concordance with Mindanao is not as close since Merrill suggests the subdivision of the island into subregions.

The consensus of earlier biogeographical research is that while Palawan served as a Asian corridor to the Philippines, Mindanao served as both an Asian and Papuan corridor to the Philippines via Sulawesi in the case of Australo-Papuan biota. However unlike in Palawan (Heaney et al. 1998), there is no tectonic evidence that Mindanao was ever connected to Borneo or Sulawesi. Thus earlier hypotheses that proposed that Australo-Papuan biotic elements dispersed to Mindanao and to the rest of the Philippines is highly unlikely. Thus the presence of Australian and Papuan biotic elements in Mindanao is likely due to the accretion of terranes rather than through dispersal. The timing of accretion can now be roughly estimated.

The questions that will be explored in this paper are the following:

- 1) What are the phylogenetic connections between Sulawesi, Wallacea and the Philippines?
- 2) Why do basal Philippine taxa have a Wallacean

connection?

- 3) Why many of these Australian and Wallacean elements did never dispersed beyond their eastern Philippine distribution?

Mindanao and Luzon hold the key to answering some of these questions due to its geological history and its particular physical geography. To look into these questions a comparative biogeography of some iconic Philippine taxa and general notes on the patterns of distribution in the Philippines especially on Luzon and Mindanao.

Methods: Comparative Biogeography

The origin of the Philippine Eagle

The Philippine Eagle *Pithecophaga jeffreyi* Ogilvy-Grant is the iconic representation of Philippine biodiversity (Collar et al. 1999). The distribution of this species is largely restricted to the eastern side of the archipelago consisting of the islands of Luzon, Samar, Leyte and Mindanao. On Luzon, it is restricted to the Sierra Madre ranges while on Mindanao, it is restricted to the eastern and central sections of the island (Denr et al. 1997; Collar et

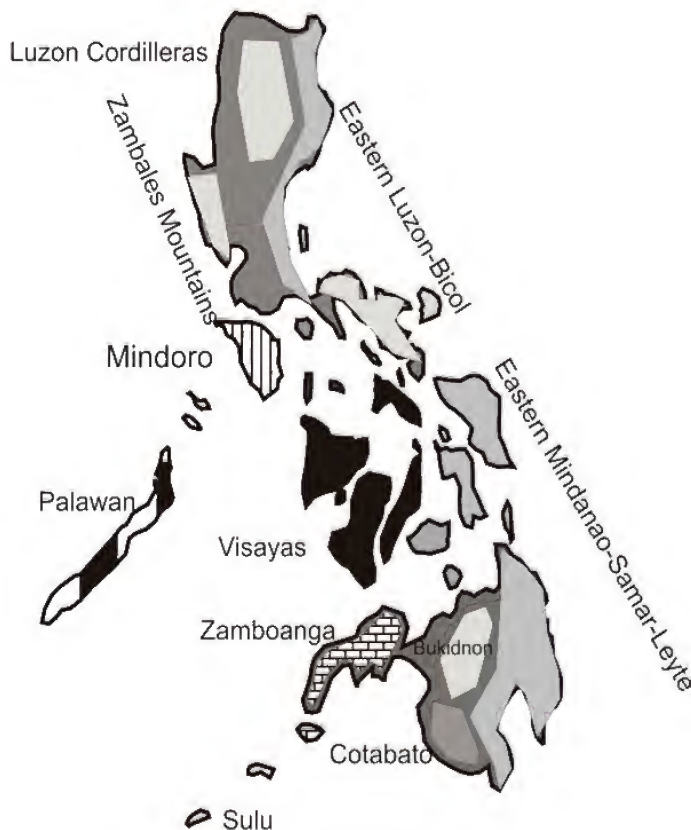


Figure 5. Floral subprovinces of the Philippines (adapted from Merrill in Dickerson 1928).

al. 1999).

The evolutionary relationship of the eagle with the neotropical Harpy eagles has been the subject of investigation since it was first formally described. Based skeletal and osteological morphology and its large size, the eagle has been classified with the Harpiinae (Shufeldt 1919), although Sharpe (1899) and Whitehead (1899) proposed an alternative classification placing the eagle with the *Circaetus* and *Spilornis* snake eagles based on the anatomy of the talons. Given its large size, similar ecological niche as top predator in closed canopy rainforests, the eagle has been traditionally classified with the harpy eagles. Living representatives of this family include the Neotropical harpy, *Harpia*, crested eagle *Morphnus*, the New Guinea Harpy *Harpyopsis*, and the Philippine *Pithecophaga*.

However recent molecular phylogenetic studies suggest that *Pithecophaga* is more closely related to the Circaetinae clade of snake eagles rather to the Harpininae harpy eagles (Lerner, Mindell 2005). The morphological, skeletal and osteological similarities of *Pithecophaga* with *Harpia* is an excellent example of convergent evolution. Both eagles occupy similar rainforest biomes and is the top predator in their habitats.

The origin of the Circaetinae provides the key to understanding the origin of the Philippine Eagle. The modern distribution of this subfamily is Afrotropical and Oriental. Based on this distribution, the subfamily can be hypothesized to have a Gondwanan origin. This is further supported that there are two clades within this subfamily. The Indomalayan clade consists of the Asian serpent eagles *Spilornis* which live in lowland tropical rainforests. The other clade is the Afrotropical clade that consists of *Circaetus* and the Bateleur *Theraptor ecaudatus*. In the Lerner and Mindell (2005) phylogenetic reconstruction of eagles, the sister taxa of *Pithecophaga* is *Theraptor* although this has weak bootstrap support. The bateleur is a raptor of the African savannah. The question is now how a member of an African clade persisted in Southeast Asia?

The Australasian origin of Philippine endemic rats

The Philippines has 22 genera and 64 species of rodents and their diversification provides an opportunity to study patterns and processes in island species radiations (Jansa et al. 2006). Ninety percent (90%) of the Philippine rodent species are endemic to the archipelago. The biogeographical

questions on the origin of the fauna are where the original colonizing species came from and what is the role of dispersal and vicariance in the development of the rodent fauna? Heaney (1986) hypothesized that the original colonizers came from the Asian mainland. The Philippine archipelago is at least 25 MY old (Yumul et al. 2008) and with the exception of Palawan, the Philippine islands were never connected to mainland Asia. Thus initial colonization may have been over water. Jansa et al. (2006) reconstructed the molecular phylogeny of Philippine rodents and concluded that there were at least two colonization episodes, one occurring at 15-20 MYA and a later one at 3 MYA. The older colonists gave rise to the Old Endemic clade while the later ones gave rise to the New Endemic clade.

The Old Endemics make up two clades with 15-25 extant species (mostly cloud rats, *Crateromys* and *Phleomys* and their relatives) and the New Endemics make 3 clades with 3 to 5 species each. The Old Endemics are mainly folivorous and vermivorous. Old and new endemics diversified within the Philippine archipelago.

Hall's (1998) tectonic reconstruction of the Philippine archipelago at 15-20 MYA reveals a geography different from today's. The proto northern Luzon landmass was separated from proto Mindanao by the marginal oceanic basin that will become the Sulu and Sibuyan seas. Since the Old Endemics are found largely on Luzon with representatives in Mindoro and Panay and if a purely dispersalist theory is assumed, then their nearest source of colonists would have been Asia. However their nearest living relatives are in Australasia and widely distributed there. The sister taxon of Old Endemic clade D is Australasian (Steppan et al. 2003) If an Asian dispersal is assumed then their ancestors would have been long extinct there (Jansa et al. 2006). The more parsimonious theory would be that their ancestors initially came from Australasia and were placed nearer to Luzon as the Philippine Plate rotated to its present position.

The origin of the Philippine Tarsier

Extant tarsier taxa have allopatric and parapatric distributions (Shekelle 2006). There is not a single case of sympatric tarsiers. Tarsiers are distributed only in Southeast Asia but their well documented fossil history suggests they were distributed widely in mainland Asia extending into northern China. The latest dated Asian fossil tarsier is from a Miocene deposit in Thailand (Ginsberg, Mein 1986).



Two clades have been proposed for tarsiers. The Western clade includes the Western Tarsier *Tarsius bancanus*, *T. bancanus borneanus*, *T. bancanus saltator* and the Philippine Tarsier *T. syrichta*. A morphological gradient can be observed among tarsiers. The western species have the largest eyes, shortest ears, longest limbs and the Philippine species has intermediate features while the eastern species have the smallest eyes, shortest limbs and longest ears (Groves 1998; Shekelle 2006). Given these characteristics, Musser and Dagosto (1987) hypothesized that there are two clades, one containing the Western/Philippine species and the other the Eastern / Sulawesi species. Molecular phylogenetic analysis supports this hypothesis (Shekelle 2001).

Unlike other taxa whose distributions provide a clear demarcation between the Indomalayan or Oriental and Australasian zoological regions, tarsiers are found on both sides of the Wallace's Line. The taxonomic and phylogenetic position of the Philippine species is puzzling. While it is considered as part of the western clade, its features are transitional between the western and eastern species. Nevertheless, it is more likely that the Philippine species was derived from the western species since its distribution never extended beyond the ice age island of Greater Mindanao. As such it is found in Samar, Biliran, Leyte, Bohol, Dinagat, Mindanao and Basilan. The western species distribution is puzzling also. *T. bancanus* is found in Borneo and the Southern tip of Sumatra but is absent on Java and Bali. Shekelle (2006) hypothesizes that the species is as tolerant of human habitat disturbance as the Philippine species. However its absence in Java even in areas not impacted by human activities such as Ujung Kulon suggests that it was never found there.

The Philippine Tarsier is likely to have originally existed as a panmictic population in Greater Mindanao. Pleistocene vicariance due to sea level rise isolated populations on Greater Mindanao islands. These isolated populations are believed to represent morphological subspecies. As for the origin of the Philippine species, it is hypothesized that it diverged from the ancestral western species at 5.6 MYA in the Miocene at the same time that the Sulawesi species diverged.

The Eastern clade consists of *T. sangirensis*, *T. pumilus*, *T. dentatus*, *T. pelegensis*, *T. lariatang* and the newly described Siau Island species *T. tumpara* (Shekelle et al. 2008). Unlike in western species, the eastern species have distinct habitat preferences. It is only on Sulawesi that a montane tarsier spe-

cies exists, *T. pumilus*. Phylogenetic reconstruction has not provided a clear hypothesis on when the Eastern species diverged from the ancestral Asian one. This probably predated the Miocene origination of the Philippine species and before the coalescence of Sulawesi into a single landmass from being an archipelago. Species diversification of Sulawesi species probably occurred before the island was formed. It is possible although unlikely that a tarsier species can cross over water from Borneo (Morley 1998). The present distribution of tarsiers suggests that is unlikely. The Philippine species has never crossed into Cebu from Bohol despite separated by less than 30 km of water during the Pleistocene. Nevertheless the biogeography of Sulawesi tarsiers is the exact opposite of those from the Philippines. On Sulawesi, island coalescence brought different species into one island, while on the Philippines vicariance separated populations.

Philippine wild pigs

Southeast Asia has the highest diversity of wild pigs in the world (Lucchini et al. 2005). This is likely due to vicariance in archipelagos where sea level transgressions caused the isolation and reconnection of islands. The Philippines is the island group with the most number of restricted distribution wild pig species with at least 5 species *Sus philippensis*, *S. barbatus*, *S. cebifrons*, *S. barbatus ahoenobarbus* (Oliver 1995). The latter has been proposed to be elevated to species status (Lucchini et al. 2005). The distribution of the extant species supports Heaney's theory on Philippine biodiversity and his division of the archipelago into faunal regions (Heaney 1986; 1998).

Wu et al. (2006) proposed a phylogeny of wild pigs based on mtDNA sequences and placed the Philippine species as a primitive group within the Eurasian clade closer to the basal African group that includes the warthog. The phylogeny reflects an ancient split between the Eurasian and African clades similar to that seen in the Circaetinae eagles. This split is consistent with the wild pig modern distribution. It is also interesting to note that the distribution of the more basal and derived clades follow an East-West pattern. The basal clades have an Eastern distribution while the derived ones have a Western distribution.

The Visayan Warty Pig *S. cebifrons* is the oldest to have diverged in the Eurasian clade followed by the Philippine Wild Pig *S. philippensis* which is also distributed in Luzon, Mindoro and Mindanao.



Each of these islands has their own subspecies with Luzon having *S. p. philippensis*, Mindoro with *S. p. oliveri* and Mindanao with *S. p. mindanensis*. *S. cebifrons* and *S. philippensis* are closely related to the Sulawesi *S. celebensis*. A possible evolutionary scenario is that the Asian ancestor crossed into the Philippines via Palawan in the Pliocene giving rise to the primitive *S. cebifrons* and *S. philippensis*. This hypothesized ancestor also crossed into Sulawesi giving rise to *S. celebensis*. The Sulawesi babirusa *Babyrussa babyrussa* is a pig that is difficult to classify with other pigs (Groves 2001) but is phylogenetically closer to the American pecary rather than to the African warthog (Wu et al. 2006). This pig species is found only in the northern end of the island. Sulawesi also has a Miocene giant pig species *Celebochoerus* whose fossils were found only to the southern Walanae region of the island. This species is closely related with similar fossil species found in Java and the Siwalik Hills of Pakistan (Groves 2001).

Philippine parrots

The Psittaciformes has a Gondwanan origin (Wright et al. 2008). Diversification in modern Southeast Asian clades coincided with the final separation of West Antarctica, South America and India in the Oligocene. Among the genera associated with this clade are the Philippine and Wallacean genera *Tanygnathus*, *Prioniturus*, *Bolbopsittacus*, and *Loriculus*. Another clade which diversified in the Miocene when Australia approached Asia includes the Wallacean-Australian genus *Trichoglossus* whose only Philippine representative is found in Mindanao at mid-elevation montane forests (Collar et al. 1999; Kennedy et al. 2000). The congeners of the Philippine species are still found in Wallacea and Sulawesi.

Biogeographic patterns in Mindanao and Luzon as revealed by plant and other animal taxa

Biogeographic research on Luzon, Mindanao and the Southern Philippines has been sparse and limited to a few taxa. However given the existing material at hand, it is possible to determine patterns of distribution common to both large islands.

The first biogeographical pattern that is very apparent is the affinities between the Eastern Luzon and Eastern Mindanao biotic regions. The two biotic regions may be considered as a transition

zone. The eastern Philippines including the Sierra Madre of Luzon, Bicol, the Greater Mindanao islands of Leyte, Samar, Dinagat, Eastern Mindanao, the Maluku islands and New Guinea form a continuous island arc (Heads 2003). In the montane plant family Ericaceae, there are a lot of direct Philippines-New Guinea affinities. In ferns 57 species are shared between these two island systems (Cope land 1950). While this island arc reflects a certain unity in floral and faunal composition, there are differences between the northern end (Luzon) and the southern end (New Guinea). Within the Philippines similar differences can be noted. For example, the Palanan rainforest plot in Isabela, north-eastern Luzon is composed mainly of a west Malesian flora rather than an eastern (Wallacean) one (Co et al. 2006). Of the 311 species noted in the plot only 10 can be considered as east Malesian. Forty six species (15% of the total) are shared with Lamber Hills in Sarawak, Malaysia. In eastern Mindanao however, the myrtaeous flora is Papuan. This flora does not have special alliances with western Malesia.

The Melastoma (Myrtales) alliance phylogeny in Tropical Asia shows this pattern quite clearly. The clade consisting of the *Astronia*, *Beccarianthus*, *Astrocalyx* and *Astronidium* genera show strong Philippine and New Guinea affinities (LaFrankie 2010). This monophyletic group is centered in New Guinea. The monotypic genus *Astrocalyx* is endemic to the eastern Philippines (Mindanao to Luzon) floral region. *Astronia* has its greatest species radiation in New Guinea (30) species followed by the Philippines (17) species. This group is primarily restricted to montane and mossy forests in eastern Luzon and Mindanao (Co et al. 2006). The distribution of mosses show the same pattern especially for Mindanao (Tan 1998). The presence of *Eucalyptus deglupta* in eastern Mindanao is also evidence of a New Guinea-Australian affinity (Ladiges et al. 2003). The similarities of the Mindanao form with that of the New Britain form in this eucalypt supports the Melanesian arc panbiogeographic track that runs through New Guinea to Mindanao.

The second biogeographic pattern common to Mindanao and Luzon is the biotic disjunction between the eastern and central regions of these two islands. Both islands have an eastern and a central mountain range and have certain floral similarities in distributional disjunction. On Luzon this is very notable in the central Cordillera flora which is more Himalayan than Malesian. Almost all the Himalayan representatives of the Luzon Cordillera flora are represented in Taiwan and southern China (Dickerson et al. 1928). This forms a separate biome whose



dominant tree is *Pinus kesiya* Royle ex Gordon. In Mindanao, the Bukidnon Highlands present similar patterns with some montane species having affinities to the Luzon Cordilleras. However most of the plant species have affinities to the New Guinea flora. This may also be the reason why the butterflies (Papilionoidea) of Mindanao and Luzon share faunal similarities in composition (Racheli et al. 1989)

The third biogeographic pattern common to Mindanao and Luzon is the presence of a western biotic region that is very distinct from the eastern one. On Luzon this is defined by the Zambales mountain range and on Mindanao by the Zamboanga Peninsula mountains. On Luzon the Zambales mountains are home to another pine species *P. merkusii* Jungh et deVries which is found also in Mindoro and Sumatra. This region has affinities to Mindoro island and its floral affinity is western Malasian with the montane flora having a distinct Himalayan component (Linis 2009). On Mindanao, the Zamboanga Peninsula is a different biogeographic region from that of Eastern Mindanao. The flora and fauna here has a strong Bornean affinity. This is very apparent in the distribution of Philippine cyprinid fish (Dickerson et al. 1928). This family of strictly freshwater fishes reach their highest diversity in Indo-China and Peninsular Malaysia. Their distribution eastwards extends only to Palawan, Mindoro, Zamboanga Peninsula and into the central Lanao plateau where the family rapidly diversified (Herre 1933). Recent studies into the phylogeography of bent toed geckos *Cyrtodactylus* suggests similar evolutionary processes of Bornean immigrants rapidly diversifying in western Mindanao (Siler et al. 2010). Similar patterns were noted by Dickerson et al. (1928) in reptiles and amphibians.

Discussion

Beyond the Pleistocene paradigm in Philippine biogeography

There is a growing consensus to revisit the present Pleistocene Aggregated Island Coalescence (PAIC) model of Philippine biogeography which is currently the paradigm (Siler et al. 2010) and used for conservation planning and priority setting (Ong et al. 2002; Catibog-Sinha et al. 2006). This is necessitated by the scale of endemic biodiversity being discovered as species inventories continue in the Philippines. Pleistocene isolation and vicariance while it shows clear patterns of endemism at a larger scale may not account for these

patterns at a smaller scale or at temporal scales that predate the Pleistocene. Researchers suggest that multi-taxon and multi-locus approach should be done to address the problem. The main thesis of the PAIC model is that colonization from mainland Asia happened rarely and when it did rapid species diversification in immigrant taxa occurred.

However in the beginnings of Philippine biogeographical science Dickerson et al (1928) already had identified distributional patterns that may merit more than a vicariance or dispersal based explanation. However as the plate tectonic theory was not existence then, the causality of these distributions and how they came to be were tenuously (or more speculatively) to the land bridge paradigm which is a theory that Alfred Russel Wallace used to explain faunal similarities in Southeast Asia.

Dickerson et al. (1928) for lack of a better theory found it difficult to test why there is a large Australian / Gondwanan element in the eastern Philippines (Luzon to Mindanao) biota which strongly suggested a land bridge connection with Sulawesi and the rest of Wallacea. Until plate tectonic theory was proposed, this was not testable. However as presented in the earlier accounts of systematic biogeography and distributional analysis, it is now possible to test the Philippines-Sulawesi-New Guinea connection and a Gondwanan origin for some of the Philippine taxa.

A first test is *Pithecophaga*. Given its position within the African clade, *Pithecophaga* has probably a Gondwanan origin. This is supported by an estimated deep divergence between the Afrotropical and Indomalayan clades which likely dates back to the Oligocene. Members of these clades are restricted to their regions with the Philippine Eagle being the sole exception. It is the only representative of the Afrotropical clade in Asia and is likely a relict species. *Spilornis* on the other hand is exclusive to Southeast Asia with most species on Wallacea and is rare throughout its range. If there were close Wallacean relatives of *Pithecophaga*, they would have likely existed in Sulawesi but are now extinct. However there are not yet reported raptor fossils to test this hypothesis

The parrots have a Gondwanan origin and the dating of the phylogenetic split that gave rise to taxa (Jönsson et al. 2008) shared between Sulawesi and the Philippines are coincident with the inferred time when these island groups started to accrete (Hall 1998). It is notable that the older clade which contains *Loriculus*, *Bolbopsittacus*, *Tanygnathus* and *Prioniturus* has a wider distribution in Wallacea and the Philippines wherein member island spe-



cies are endemic and can be accounted for PAIC theory thereby fulfilling Wallace's biogeographic predictions. The younger clade containing *Trichoglossus* has a Philippine representative restricted to Mindanao and was never able to disperse to Luzon whereas members of the clade are found in Australia, New Guinea and the Maluku islands. A similar pattern can be noted in the pigs which have a Eurasian-African origin but relicts of an older radiation are found in Sulawesi and the Philippines. These basal clades are closer to the more primitive African warthog and neotropical peccaries.

The Gondwanan connections in *Pithecophaea*'s Afrotropical clade, the parrot clades, the basal pig clades are starting to become apparent. As for the bird species radiation in Wallacea, there is some evidence to show at least for the avian family Camphephagidae that colonization from Africa via the Indian Ocean was likely during the Miocene (Jönsson et al. 2008).

The biogeography of the tarsiers are interesting for they have a continental Asian ancestry and straddle Wallace's Line but the Philippine species *T. syrichta* is probably derived from the Bornean species and is restricted to the Mindanao faunal region. However tarsiers reach their highest species diversity in Sulawesi and adjacent islands. The relationship of the Philippine species with the Sulawesi species is unresolved and an answer to this is to date when the hypothetical ancestor that gave rise to the Philippine and Sulawesi species crossed from Borneo to proto-Mindanao or to the islands that would become the single island of Sulawesi. If a crossing over from Borneo to proto-Mindanao is possible then it may be possible to cross over from proto-Sulawesi to Mindanao. Dickerson et al (1928) were puzzled by the absence of marsupials in Mindanao given that they exist in the Maluku islands, Sulawesi and New Guinea and the strong botanical affinity between Sulawesi, New Guinea and the Philippines. However it is more likely that marsupials got to proto-Sulawesi at an earlier date in the Oligocene to Miocene (Moss et al. 1998) than when Mindanao was formed and they were not able to disperse (Michaux 1994).

It is most likely that the formation of the Makassar Straits between Sulawesi and Borneo in the Palaeocene and Eocene may have allowed for the dispersion of taxa such as the hypothesized ancestral Tarsier and basal pig species across a hypothesized land bridge or a series of emergent volcanic islands to western and Southern Sulawesi (Moss et al. 1998). A similar feature may have allowed for a Sulawesi-Mindanao biotic interchange

via the north arm of Sulawesi. There is a chain of volcanic arc islands that lead to Mindanao. Alternatively, Australian biotic elements may have colonized northern Sulawesi via the eastern Philippines route from the Sangihe islands and New Guinea. This hypothesis supports the contention stated in this paper that the endemic rodent genera in the Philippines is likely to have an Australasian origin. It is also supported by the presence insect taxa that are common to New Guinea and eastern Philippines but are rare or absent in Sulawesi (Gressitt 1956). However this does not answer the question of Dickerson et al (1928) on the absence of marsupials in the Philippines which are believed unable to disperse over water. Marsupials in some Wallacean islands may have been dispersed by humans rather than by natural means (Oosterzee 1997)

The third question posited in this paper is why many of the Wallacean elements seemed to have never dispersed much beyond the eastern Luzon and eastern Mindanao biotic region. A comparison with Sulawesi biogeography is relevant here. Sulawesi as a coalesced archipelago shows a high degree of faunal endemism in its various "arms". In Sulawesi, lowland and montane rainforest taxa hardly are found beyond their respective regions of endemism as best demonstrated by the tarsiers, *Macaca* monkeys, toads (Evans et al. 2009) and the basal pigs which includes the babirusa *Babirusa babirusa* (Groves 2001). A similar pattern is likely to hold for eastern Philippines, which is characterized by a wetter climate with more evenly distributed rainfall than what is known from the western side. Also a similar observation can be made for the Philippine cyprinids which are associated with the microcontinental blocks of Zamboanga, Mindoro and Palawan. These fish hardly ever dispersed beyond these terranes.

The biogeography of Luzon, Mindanao, the rest of the Philippines and Sulawesi while both about island coalescence shows difference in histories. The Philippine islands came into close proximity but were never fully coalesced thus allowing for vicariant speciation to happen. Sulawesi's constituent islands fully coalesced into single landmass but habitat and climate differences allowed for vicariance to happen. Sulawesi has more of the basal mammal lineages than the Philippines. Like in the Philippine case (Jansa et al. 2006), the sources of Sulawesi endemic species came from an old endemic colonization and a new endemic colonization (Ruedi et al. 1998).



The Philippines as part of Wallacea: a panbiogeographic model

Merrill in Dickerson (1928) places the Philippines within Wallacea given the biogeographic characteristics of the archipelago. He puts much emphasis on the “great differences in geologic history” of the various islands of Wallace’s Malay Archipelago. This region is geologically unstable and was interpreted to be a zone of transition rather than a separating line between the Asian and Australian biogeographic regions. A key observation of Merrill is that the region has a lot of relict forms which given the limited phylogenies published, appears to have a largely Gondwanan affinity.

At present Wallace’s and Weber’s lines are interpreted as a plate tectonic boundary (Audley-Charles 1981). Given the current paradigm, the tectonic history of the Philippines and the rest of Wallacea has been reconstructed (Hall 1996; 1998). However determining which oceanic or continental block was emergent is difficult during the process of tectonic evolution. Thus biogeographic interpretation has to have caveats. Most of the Philippine islands are *de novo* oceanic islands as evidenced by ophiolitic arc rocks (Hall 1996; Yumul et al.

2008) and were attached to the Philippine plate which rotated clockwise.

This tectonic rotation of the Philippine plate is so important in defining the Philippines as part of Wallacea. Present day Wallacea is shaped like a triangle with the Philippines at its apex and the base is Indonesia and New Guinea. While Merrill in Dickerson (1928) hypothesized that biotic dispersal was along the longer sides of the Wallacean triangle rather than across it. The present tectonic reconstructions show that plate rotation occurred and the proto-islands of the Philippines were translated from subequatorial latitudes to the more northern latitudes. This can be modelled using panbiogeographic approaches rather than by dispersal or vicariance as previously assumed. The panbiogeographic tracks describing Philippine and New Guinea relationships have been modelled as consistent with plate tectonic reconstructions (Heads 1990; 2001; 2003). Panbiogeographic tracks seem to be associated with the eastern Philippines terranes and microcontinental blocks such as Mindoro, Panay Cordilleras, Palawan and Zamboanga Peninsula (Fig. 6). For the microcontinental blocks, there are floral and faunal affinities with Indo-China and Sumatra. It is worth noting that

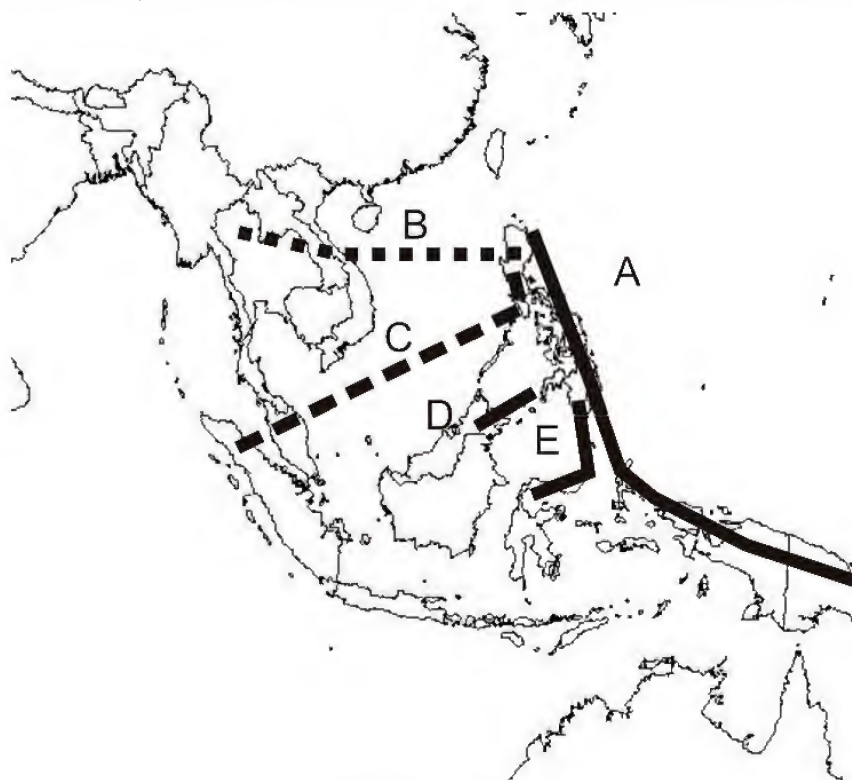


Figure 6. Hypothetical tracklines.

A - New Guinea-Banda-Eastern Philippines arc, B - Vietnam-Luzon, C - Sumatra-Mindoro-Zambales Mountains, D - Borneo-Zamboanga Peninsula, E - Sulawesi-Central Mindanao.



centres of endemism in the Philippines are associated with crustal boundaries and accretions and is clearly shown in Wallacean *Eucalyptus* which is associated with arc terranes (Ladiges et al. 2003). This is a key prediction of panbiogeography (Croizat 1958; 1964; Croizat et al. 1974; Heads 2002).

Conclusion

While the Philippines have a large Sundaland biotic component, there is a significant Wallacean, New Guinea and Australian element in the biota. The evolutionary relationships of some of the iconic taxa suggest a Wallacean and an older Gondwanan origin. Given the tectonic history of the Philippines, the evolutionary history of Wallacean taxa can be modelled using panbiogeography. Many of the taxa are associated with tectonic features and hardly dispersed beyond these. A major observation is that the basal members of the taxa discussed in this paper persist in Wallacea. This supports Merrill's in Dickerson (1928) observation that many relict taxa survive in Wallacea.

Luzon and Mindanao are keys to understanding Wallacean biogeography especially in understanding the Sundaland and Australian biotic transition. There is a need for more phylogenetic research to describe the evolutionary relationships between Philippine especially Mindanao taxa with that of Sulawesi. The following questions that date back to Dickerson and Merrill have not been fully answered. Did Luzon and Mindanao contribute to the biodiversity of Sulawesi and the rest of Wallacea? How did Wallacea and Sulawesi contribute to the biodiversity of Luzon? These questions have direct bearing on human evolution in Wallacea. It is likely that Merrill in Dickerson (1928) hypothesis on phylogenetic relicts persisting in Wallacea is supported by the discovery of the late Pleistocene survival of hominins like *Homo floresiensis* (Brown et al. 2004) and the possibility that similar archaic *Homo* existing in northern Luzon in the early to mid Pleistocene (Mijares et al. 2010). However there is still a need for more intensive biotic surveys of the Philippines and Wallacea in order to resolve these questions.

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This book chapter is dedicated to the memory of the Filipino botanists Leonard Co (1953-2010) and Daniel Lagunza (1957-2010).

References

- Audley-Charles M.G. 1981. Geological history of the region of Wallace's Line. In: Whitmore T.C. (ed.) *Wallace's Line and Plate Tectonics*. Clarendon Press, Oxford: 24-35.
- Brown P., Sutikna T., Morwood M.J., Soejono R.P., Jatmiko, Wayhu, Saptomo E, Awe Due R. 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. – *Nature* **431**, No. 7012: 1055-1061.
- Catibog-Sinha C., Heaney L.R. 2006. *Philippine Biodiversity: Principles and Practice*. Quezon City, Haribon Foundation for the Conservation of Nature: 495 pp.
- Co L., LaFrankie J., Lagunza D., Pasion K., Consunji H., Bartolome N., Yap S., Molin, J., Tongco M., Ferreras U., Davies S., Ashton P. 2006. *Forest Trees of Palanan, Philippines*. Quezon City, Center for Integrative and Development Studies, University of the Philippines, Diliman, Quezon City: 313 pp.
- Collar N., Mallari N.A., Tabaranza B.R. 1999. *Threatened Birds of the Philippines*. Bookmark, Manila: 555 pp.
- Copeland E. 1950. The origin of the Philippine fern flora. – *Philippine Journal of Science* **79**: 1-5.
- Croizat L. 1958. *Panbiogeography*. Caracas, privately published: 275 pp.
- Croizat L. 1964. *Space, time and form: The biological synthesis*. Caracas, privately published: 881 pp.
- Croizat L., Nelson G., Rosen D.E. 1974. Centers of origin and related concepts. – *Systematic Zoology* **23**, No. 2: 265-287.
- DENR-UNEP 1997. *Philippine Biodiversity. An assessment and action plan*. Makati, Bookmark: 298 pp.
- Dickerson R., Merrill E.D., McGregor R.C., Schultze W., Taylor E.H., Herre A.W. 1928. *Distribution of Life in the Philippines*. Manila, Bureau of Science: 322 pp.



- Dimalanta C.B., Suerte L., Yumul G., Tamayo R., Ramos E. 2006. A Cretaceous supra-subduction oceanic basin source for Central Philippine ophiolitic basement complexes: Geological and geophysical constraints. – *Geosciences Journal* **10**, No. 3: 305-320.
- Evans B.J., Supriatna J., Andayani N., Setiadi M.I., Cannatella D.C., Melnick D.J., Yoder A. 2009. Monkeys and toads define areas of endemism on Sulawesi. – *Evolution* **57**, No. 6: 1436-1443.
- Faustino D.V., Yumul G.P., de Jesus J.V., Dimalanta C.B., Aitchinson J.C., Zhou M.-F., Tamayo R.A., Leon M.M. 2003. Geology of southeast Bohol, central Philippines: accretion and sedimentation in a marginal basin. – *Australian Journal of Earth Sciences* **50**: 571-583.
- Ginsberg L., Mein P. 1986. *Tarsius thailandica* nov sp. Tarsiidae (Primates, Mammalia) fossile d'Asie. – *Comptes rendus d'I Academie de Science (Paris)*, Series II, **2**, No. 19: 1213-1215.
- Gressitt J. 1956. *New Guinea and Insect Distribution*. Proceedings of the Tenth International Congress of Entomology, Montreal, PQ, Canada: 767-773.
- Groves C. 1998. Systematics of Tarsiers and Lorises. – *Primates* **39**, No. 1: 13-27.
- Groves C. 2001. Mammals in Sulawesi: Where did they come from and when, and what happened to them when they got there? In: Metcalfe I., Smith J.M., Morwood M., Davidson I (eds.) *Faunal and Floral Migrations and Evolution in SE Asia and Australasia*. AA Balkema Publishers, Tokyo: 332-342.
- Hall R. 1996. Reconstructing Cenozoic SE Asia. In: Hall R., Blundell D. (eds.) *Tectonic Evolution of Southeast Asia 1*. Geological Society of London, London: 153-184.
- Hall R. 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall R., Holloway J.D. (eds.) *Biogeography and Evolution of SE Asia*. Backhuys Publisher, Leiden: 99-131.
- Heads M.J. 1990. Mesozoic tectonics and the deconstruction of biogeography: a new model of Australasian biology. – *Journal of Biogeography* **17**: 223-225.
- Heads M.J. 2001. Birds of paradise (Paradisaeidae) and bowerbirds (Ptilonorhynchidae): regional levels of biodiversity and terrane tectonics in New Guinea. – *Journal of the Zoological Society London* **225**: 331-339.
- Heads M. 2002. Regional patterns of biodiversity in New Guinea animals. – *Journal of Biogeography* **29**: 285-294.
- Heads M.J. 2003. Ericaceae in Malesia. – *Telopea* **10**, No. 1: 311-449.
- Heaney L.R. 1986. Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. – *Biological Journal of the Linnean Society* **28**: 127-165.
- Heaney L.R. 1998. The origins and dimensions of biodiversity in the Philippines In: Heaney L.R., Regalado J.C., Jr. (eds.) *Vanishing Treasures of the Philippine Rainforest*. Chicago, Field Museum of Natural History: 12-22.
- Heaney L.R. 1999. Historical biogeography in SE Asia: integrating paradigms and refining the details. – *Journal of Biogeography* **26**: 435-437.
- Heaney L.R. 2000. Dynamic disequilibrium: A long term, large scale perspective on the equilibrium model of island biogeography. – *Global Ecology and Biogeography* **9**, No. 1: 59-74.
- Heaney L.R. 2004. Conservation biogeography in oceanic archipelagoes. In: Lomolino M.V., Heaney L.R. (eds.) *Frontiers of Biogeography: New Directions in the Geography of Nature*. Sinauer Publishers, Sunderland MA: 345-360.
- Heaney L.R., Regalado J.C. 1998. *Vanishing Treasures of the Philippine Rainforest*. Chicago, The Field Museum of Natural History: 88 pp.
- Heaney L.R., Rickart E.A. 1990. Correlations of clades and clines: Geographical, elevational and phylogenetic patterns in Philippine mammals. In: Peters G., Hutterer R. (eds.) *Correlations of clades and clines: Geographical, elevational and phylogenetic patterns in Philippine mammals. Vertebrates in the Tropics*. Museum Alexander Koenig, Bonn: 321-322.
- Heaney L.R., Walsh J.S., Jr, Townsend-Peterson A. 2005. The roles of geological history and colonization abilities in genetic differentiation between mammalian populations in the Philippine archipelago. – *Journal of Biogeography* **32**: 229-247.
- Herre A.W. 1933. The fishes of Lake Lanao, a problem in evolution. – *American Naturalist* **67**, No. 709: 154-162.
- Jansa S.A., Barker F.K., Heaney L.R. 2006. The pattern and timing of diversification in Philippine endemic rodents: Evidence from mitochondrial and nuclear gene sequences. – *Systematic Biology* **55**, No. 1: 73-88.
- Jönsson K.A., Irestedt M., Fuchs J., Ericson P.G.P., Christidis L., Bowie R.C.K., Norman J.A., Pasquet E., Fjeldsa J. 2008. Explosive avian radiations and multi-directional dispersal across Wallacea: Evidence from the Campephagidae and other Crown Corvida (Aves). – *Molecular Phylogenetics and Evolution* **47**, No. 1: 221-236.
- Kennedy R.S., Gonzales P.C., Dickinson E.D., Miranda H.C., Jr, Fisher T.H. 2000. *A Guide to the Birds of*



- the *Philippines*. Oxford, Oxford University Press: 540 pp.
- Ladiges P.Y., Udovicic F., Nelson G. 2003. Australian biogeographical connections and the phylogeny of large genera in the plant family Myrtaceae. – *Journal of Biogeography* **30**: 989-998.
- LaFrankie J.V. 2010. *Trees of Tropical Asia*. San Fernando, La Union, Black Tree Publications, Inc.: 750 pp.
- Lerner H.R.L., Mindell D.P. 2005. Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. – *Molecular Phylogenetics and Evolution* **37**: 327-346.
- Linis V. 2009. Biogeography of Mindoro mosses. – *Blumea* **54**: 290-296.
- Lucchini V., Meijaard E., Diong C.H., Groves C.P., Randi E. 2005. New phylogenetic perspectives among species of South-east Asian wild pig (*Sus* sp) based on mtDNA sequences and morphometric data. – *Journal of the Zoological Society London* **266**: 25-35.
- MacArthur R.M., Wilson E.O. 1967. *The Theory of Island Biogeography*. Princeton, Princeton University Press: 203 pp.
- Mayr E. 1976. Wallace's Line in the Light of Recent Zoogeographic Studies. In: Mayr E. (ed.) *Evolution and Diversity of Life*. Harvard University Press, Cambridge MA: 626-645.
- McDermott F., Francisco F., Jr., Defant M., Turner S., Maury R. 2005. The petrogenesis of volcanics from Mt. Bulusan and Mt. Mayon in the Bicol arc, the Philippines. – *Contributions to Mineralogy and Petrology* **150**, No. 6: 652-670.
- Merrill E.D. 1923. Distribution of the Dipterocarpaceae. Origin and Relationships of the Philippine Flora and Causes of the Differences between the Floras of Eastern and Western Malaysia. – *Philippine Journal of Science* **23**: 1-23.
- Michaux B. 1994. Land movements and animal distributions in east Wallacea (eastern Indonesia, Papua New Guinea and Melanesia). – *Palaeogeography, Palaeoclimatology, Palaeoecology* **112**, No. 3/4: 323-343.
- Middleton C., Buenavista A., Rohrlach B., Gonzalez J., Subang L., Moreno G. 2004. A Geological Review of the Tampakan Copper-Gold Deposit, Southern Mindanao, Philippines. In: Maul J.L. (ed.) *Hi Tech and World Competitive Mineral Success Stories Around the Pacific Rim*. Proceedings of PACRIM 2004 Conference, Adelaide, 19-22 September, 2004, AusIMM, Melbourne: 173-187.
- Mijares A.S., Détoit F., Piper P., Grün R., Bellwood P., Aubert M., Champion G., Cuevas N., De Leon A., Dizon E. 2010. New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. – *Journal of Human Evolution* **59**, No. 1: 123-132.
- Morley R. 1998. Palynological evidence for tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In: Hall R., Holloway J.D. (eds.) *Biogeography and Geological Evolution of SE Asia*. Backhuys Publisher, Leiden: 211-234.
- Moss S.J., Wilson M.E. 1998. Biogeographic implications of tertiary paleogeographic evolution of Sulawesi and Borneo. In: Hall R., Holloway J.D. (eds.) *Biogeography and Evolution of SE Asia*. Backhuys Publisher, Leiden: 133-163.
- Musser G., Dagosto M. 1987. The identity of *Tarsius pumilus*, a pygmy species endemic to the montane mossy forests of central Sulawesi. – *American Museum Novitates* **2867**: 1-53.
- Oliver W. 1995. The taxonomy, distribution and status of Philippine wild pigs. – *Ibex* **3**: 26-32.
- Ong P., Afuang L., Rosell-Ambal R. 2002. *Philippine Biodiversity Conservation Priorities: a second iteration of the National Biodiversity Strategy and Action Plan*. Manila, DENR, CI, UPCIDS and FPE: 113.
- Oosterzee P. von 1997. *Where Worlds Collide: The Wallace Line*. Melbourne, Reed Publishing: 234 pp.
- Queaño K.L., Ali J.R., Pubellier M., Yumul J.G.P., Dimalanta C.B. 2009. Reconstructing the Mesozoic-early Cenozoic evolution of northern Philippines: clues from palaeomagnetic studies on the ophiolitic basement of the Central Cordillera. – *Geophysical Journal International* **178**, No. 3: 1317-1326.
- Racheli T., Biondi M. 1989. Biogeographical observations on the Philippine Papilionoidea (Lepidoptera). – *Italian Journal of Zoology* **56**, No. 4: 333-347.
- Ruedi M., Auberson M., Savolainen V. 1998. Biogeography of Sulawesi Shrews: Testing for their Origin with a Parametric Bootstrap on Molecular Data. – *Molecular Phylogenetics and Evolution* **9**, No. 3: 567-571.
- Sharpe R.B. 1899. *Hand-list to the genera and species of birds*. London, The British Museum: 677 pp.
- Shekelle M. 2006. Distribution and biogeography of tarsiers. In: Shekelle M., Maryanto C., Groves C., Schulze H., Snider H.F. (eds.) *Primates of the Oriental Night*. Indonesian Institute of Sciences (LIPI), Jakarta: 13-27.
- Shekelle M., Groves C., Merker S., Supriana J. 2008. *Tarsius tumpara*: a new tarsier species from Siau Island, North Sulawesi. – *Primate Conservation* **23**: 55-64.
- Shufeldt R.W. 1919. Osteological and other notes on the monkey-eating eagle of the Philippines *Pithecopphaga jeffreyi* Grant. – *Philippine Journal of Science* **15**, No. 1: 31-58.
- Siler C.D., Oaks J.R., Esselstyb J. A., Diesmo, A.C.,



- Brown R.M. 2010. Phylogeny and biogeography of Philippine bent-toed geckos (Gekkonidae: *Cyrtodoactylus*) contradict a prevailing model of Pleistocene diversification. – *Molecular Phylogenetics and Evolution* **55**: 699-710.
- Simpson G.G. 1977. Too many lines. – *Proceedings of the American Philosophical Society* **121**, No. 2: 107-120.
- Steppan S.J., Zawadzki C., Heaney L.R. 2003. Molecular phylogeny of the endemic Philippine rodent *Apomys* (Muridae) and the dynamics of diversification in an oceanic archipelago. – *Biological Journal of the Linnean Society* **80**, No. 4: 699-715.
- Tan B.C. 1998. Noteworthy disjunctive patterns of Malesian mosses. In: Hall R., Holloway J.D. (eds.) *Biogeography and Evolution of SE Asia*. Backhuys Publisher, Leiden: 235-241.
- Vogel T., Flood T., Patino L., Wilmot M., Maximo R., Arpa C., Arcilla C., Stimac J. 2006. Geochemistry of silicic magmas in the Macolod Corridor, SW Luzon, Philippines: evidence of distinct, mantle-derived, crustal sources for silicic magmas. – *Contributions to Mineralogy and Petrology* **151**, No. 3: 267-281.
- Wallace A.R. 1859. On the zoological geography of the Malay Archipelago. – *Zoological Proceedings of the Linnaean Society*. <http://www.wku.edu/~smithch/wallace/S053.htm> (last accessed: 12 October, 2009)
- Wallace A.R. 1880. *Island Life: The Phenomena and Causes of Insular Faunas and Floras*. London, McMilland and Co: 560 pp.
- Wright T.F., Schirtzinger E.E., Matsumono T., Eberhard J., Graves G.R., Sanchez J.J., Capelli S., Muller H., Scharpegge J., Chambers G.K. Fleischer, R.C. 2008. A multilocus molecular phylogeny of the Parrots (Psittaciformes): Support for a Gondwanan origin during the Cretaceous. – *Molecular Biology and Evolution* **25**, No. 10: 2141-2156.
- Wu G.-S., Pang J.-F., Zhang Y.-P. 2006. Molecular phylogeny and phylogeography of Suidae. – *Zoological Research* **27**, No. 2: 197-201.
- Yumul G.P., Dimalanta C.B., Maglambayan V.B., Marquez E.J. 2008. Tectonic setting of a composite terrane: a review of the Philippine island arc system. – *Geosciences Journal* **12**: 7-17.
- Yumul G.P., Dimalanta C.B., Tamayo R.A., Baretto J.A.L. 2000. Contrasting morphological trends of islands in Central Philippines. – *The Island Arc* **9**, No. 4: 627-637.
- Yumul G.P., Dimalanta C.B., Tamayo R.A., Maury R.C., Bellon H., Polve M., Maglambayan V.B., Querubin C.L., Cotten J. 2004. Geology of the Zamboanga Peninsula, Mindanao, Philippines: an enigmatic South China continental fragment? – *Geological Society, London, Special Publications* **226**: 289-312.
- Zamoras L.R., Montes M.G.A., Queaño K.L., Marquez E.J., Dimalanta C.B., Gab, J.A.S., Yumul G.P. 2008. Buruanga peninsula and Antique Range: Two contrasting terranes in Northwest Panay, Philippines featuring an arc-continent collision zone. – *Island Arc* **17**, No. 4: 443-457.

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